



A mathematical model of growth of population of fish in the larval stage: Density-dependence effects

Ovide Arino ^a, My Lhassan Hbid ^b, Rafael Bravo de la
Parra ^{c,*}

^a *Department of Mathematics, I.P.R.A., University of Pau, 1 av de l'Université 64 000 Pau, France*

^b *S.P.D.S.L. Department of Mathematics, Faculty of Sciences, University Cadi Ayyad, B.P. S15,
Marrakesh, Morocco*

^c *Departamento de Matemáticas, Universidad de Alcalá, 28871 Alcalá de Henares (Madrid), Spain*

Received 11 October 1996; received in revised form 8 January 1998

Abstract

A mathematical model for the growth of a population of fish in the larval stage is proposed. The emphasis is put on the first part of the larval stage, when the larvae are still passive. It is assumed that during this stage, the larvae move with the phytoplankton on which they feed and share their food equally, leading to ratio-dependence. The other stages of the life cycle are modeled using simple demographic mechanisms. A distinguishing feature of the model is that the exit from the early larval stage as well as from the active one is determined in terms of a threshold to be reached by the larvae. Simplifying the model further on, the whole dynamics is reduced to a two dimensional system of state-dependent delay equations. The model is put in perspective with some of the main hypotheses proposed in the literature as an explanation to the massive destruction which occurs between the egg stage and the adult stage. © 1998 Elsevier Science Inc. All rights reserved.

* Corresponding author. Tel.: +34-91 885 4903; fax: +34-91 885 4951.

1. Introduction

To describe the problem which motivated the present work, let us quote an estimate gleaned in the very interesting monograph that Horwood ([1], p. 291) has devoted to the Bristol Channel sole: “One egg in 1–2 million will survive to the mean age of adulthood”. The massive regulation mechanisms of the abundance of many fish populations that have maintained most harvested species around positive equilibrium for as long as abundance of such species has been documented are still mostly unknown, and, at the least, subject to controversies. Where, along the life history of fish from the egg to adult, does the huge destruction take place? The answer to this question is probably not unique: it depends on many factors including the species themselves, their habitat, the temperature etc. In Leggett and Deblois [2], the main hypotheses regarding survival and death mechanisms are reviewed. This includes the Hjort critical period, see Ref. [3], the Cushing ‘match–mismatch’ hypothesis, see Ref. [4]; the food abundance vs. feeding success (it is not sufficient that food be present, it is also essential that the larvae be able to catch it). None of these hypotheses seems to be indisputably superior to the others. One could take as an obvious statement that some of the effects on the survival might be tested in laboratory experiments. However, great care must be exercised when comparing field and real data with such laboratory data. MacKenzie et al. [5] made observations that indicate striking differences in ingestion rates in field/laboratory conditions. Regner [6] suggests that laboratory experiments so designed to test the effects of currents and waves on the survival of eggs may be too harsh, compared to real life conditions. It is widely admitted that most of the destruction occurs before the first feeding period, both by egg damage [6] and by predation and cannibalism [7–10]. Starvation during the larval stage [3,11,12] is considered the other main cause of mortality. Which of these causes is dominant is still a matter of investigation. In Ref. [2], it is reported from Bailey and Houde [13] that “the question of whether starvation or predation is more important as a cause of early life mortality remains unresolved, and there may be no unequivocal answer because the situation may vary with species, area, and year”.

How important early mortality is, in the overall mortality, is also not resolved yet. Lagardère [14] reports a decision taken some years ago to prohibit fishing in some bay. After fishing was permitted again in the bay, fishermen were surprised to capture a high percentage of small fishes. This suggests that the recruitment in the juvenile stage is probably higher than generally believed. Returning to mortality before feeding, a recent report by Dorsey et al. [10], based on field studies of eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay concludes that more than 93% of bay anchovy daily cohorts die within two days after egg fertilization and before larvae reach the first-feeding stage. The estimates are based on the fact that eggs hatch <24 h after being spawned, which allows to estimate the decline on a single day.

There is, however, a lot of uncertainty on such estimates, due to the fact that the eggs do not correspond to instantaneous cohorts, some diffusion is taking place, and not all the places can be considered equal with respect to mortality, which varies significantly between sites and days (from 2% to 98%). Going from samples to a general estimate requires a model. If, however, the death toll of the pre-larval stage is as high as indicated, death at the larval stage should be less harsh and possibly be based more on mechanisms internal to the larval stage (density-dependence, unfavorable feeding conditions) than on predation by other species or by more advanced stages.

Our impetus for building a model of growth and survival at the early larval stage came as part of an actual effort to understand the incredible challenge recalled at the beginning. The scenario we model is the following: early larvae are mainly distributed in small or large patches, being themselves subpatches of larger patches of plankton. Such patches form the upper part of the thermocline, where they are stirred up by small turbulence and are then carried in ensemble by transport, as long as they are not dispersed by ‘adverse’ weather conditions. Assuming favorable weather conditions, one can consider that the success or the failure of larvae through this first stage – where they are assumed passive – depends on the abundance of the plankton environment in which they ‘emerged’. An experimental justification of the importance of larvae patches is provided by O’Connell [12], who describes field experiments during which patches of starving larvae of northern anchovy, *Engraulis mordax*, were collected. Incidentally, O’Connell suggests determining a ‘starvation ratio’ based on collections of starving larvae, as a measure of prerecruitment in the post larval stage.

The model we propose below is essentially centered around cohorts carried with their nutrient. It is focused on the early larval stage (passive larvae), which we will denote (S1). According to the scenario we have in mind, the main cause of mortality during (S1) is density-dependence. In order to study the behavior on several years, it is necessary to model the other stages and possibly determine a renewal equation. We do this using a model for the description of the motile larvae, the juveniles and the adults. For this part, we follow closely the principles of a previous model for the sole (*Solea solea* L.) described in Ref. [15]. Under some simplifying assumptions, we obtain a renewal equation for the (S1) stage (that is to say, an equation which gives (S1) larvae of a given year in terms of the larvae of the same stage of previous years). Further aspects of the model will be presented in Section 2. We would like to underline now the sort of model it is and what it is not, and how it compares to others. What we come up with is a mathematical model, made up of several equations: equations describing the demography of each stage and equations describing the food uptake of cohorts. In doing so we obtain a rather complicated family of equations, when compared to the typical differential equations so popular in the context of fishery management, or their discrete analogues: Refs. [16–

19]. However, we maintain a level of detail low enough to allow further analytical investigation of the equations. Such equations lead to state-dependent delay differential equations: dynamical features of such equations have only recently received attention. In Ref. [20], an equation of the same type as Eq. (37) was considered, and results about oscillatory behavior and existence of periodic solutions were obtained. Such results in the context of fisheries may give interesting insights on situations where uniformly good abiotic conditions would prevail during a number of years or could even be adapted to changing abiotic conditions.

It is quite a common practice in population dynamics to assume that the size (or, weight) is governed by a differential equation (see, for example, Ref. [21]). What we assume here is that the growth is a function of the age and the population occupying a certain volume. The latter expresses the density-dependent effect on the survival, an idea which, in the context of fisheries, goes back to Ricker and Foerster who, in Ref. [22] write that “density-dependent growth affects cumulative mortality”. We chose the simplest form of density-dependence, that is, inverse relationship to the number of larvae per unit of volume. This is the same kind of non-linearity as in a model introduced previously by Shepherd and Cushing [23] (see Ref. [24] for a comprehensive account of size specific theory of early life in fishes). However, the Shepherd and Cushing model differs from ours in the sense that it structures the fish of a same year by weight irrespectively of the age in the year. Instead, the structuring variable in our model is the age, not the weight. The weight (or, rather, the amount of food ingested since the beginning of larval stage) is the factor which determines whether or not a larva will proceed to the next stage (assuming that it has not died from any other cause). This is the other distinguishing feature of our model: the passage from passive larval stage to the next one (active larvae) is subject to the cumulative food uptake reaching a certain threshold value. We may also impose a time limit T_1 , that is, the threshold should be reached within T_1 . A threshold of the same nature is also assumed to control the passage from the active larval stage to the juvenile stage.

Amongst other approaches, a very tempting one uses functional relationships between parameters characteristic of either the fish (length, weight, respiration, etc.) and/or environmental parameters (temperature, salinity, etc.), that is, allometric relations [24]. Such formulae are very appealing. But, first of all, they are valid only on average, and their utilization in a specific example should be subject to the study of some statistical relevance. On the other hand, such relationships may underlie or even hide complex mechanisms. As an example, there is a relation in Ref. [25] which shows that mortality increases with temperature. This sort of correspondence may in fact underlie an indirect predator effect: temperature increases growth, which in turn increases the vulnerability of larvae to predators. Computer simulation modelling is another approach which has been gaining popularity within the last few years in the wider context

of population ecology [26]. Recently, a computer simulation, built on the principle of ‘individual-based modelling’ has been used in the study of density-dependence effects in fish populations [27,28]. In such an approach, the experimental field is substituted for by an artificial computer world where several hundreds (or, thousands) of fishes are generated, the various events undergone by individual fish (encounters with prey, motion, death, etc.) are modelled by random procedures. Each individual is given a certain number of traits (age, weight, length,...) which are modified at each run according to the outcomes of the random procedures. Several relationships are described in terms of known allometric relationships [24]. For example, the energy consumed in respiration is described as a function of the temperature, fish length and some other quantities [27]. Such simulation models are very convenient in allowing the use of powerful and fast computer simulations, with the potential of providing insight on the real life phenomenons. They, however, are also subject to criticisms and should, in our opinion, not be considered as a substitute to all other forms of modeling. One of the deficiencies is that they tend to be too complicated to allow the sort of qualitative study that mathematical models give. They are based on a number of empirical relationships and probability processes, which entail uncertainties on the value and the significance of the results.

Our approach is individually based as in the DeAngelis et al. [27]: ideally, we would like to decompose the whole life of a fish into a superposition of elementary actions, elicited by physical or biological processes. This work is a first step in this direction. The main tool in our investigations is mathematical analysis of our model. We believe that such an analysis may still give interesting results that, in particular, cannot be reached by simulation techniques. Let us briefly describe the contents of the next sections. As mentioned above, the main focus of the paper is on the early larval stage, starting just after the yolk-sac has been consumed and until the larva becomes active. We denote (S1) the early stage (passive larvae). Section 2 is devoted to the presentation of the model: the main part consists of equations describing the dynamics of the (S1) stage interacting with the dynamics of the food present in the unit of volume. Equations of the population in all of the other stages are also given. Section 3 deals with the renewal equation associated with the model. Section 4 focuses on a simplified model. A short discussion is given in Section 5.

2. Description of the model

Since we are not considering spatial effects here, we assume that the species has a uniform distribution with respect to space and we normalize the number of individuals of every stage to the number per unit of volume.

The structure of the model is the same as the one described in Ref. [15] for the sole of the Bay of Biscay. This latter model was derived from field data and

the information taken notably from Refs. [29,30]. We denote $B(t)$ the density of eggs laid per unit of volume at time t . Throughout the paper, t will denote the chronological time starting from the first day of the reproduction period of a given year. The number of eggs laid within the interval $[t_1, t_2]$ in a unit of volume is $\int_{t_1}^{t_2} B(t) dt$.

In Ref. [15], it is assumed that eggs are immediately transformed into larvae which start to move both in the water column and horizontally. Here, $L(a, t)$ will denote the corresponding density of motile larvae: $\int_{a_1}^{a_2} L(a, t) da$ will be the number of such larvae with age between a_1 and a_2 , per unit of volume. An additional stage is introduced between the eggs and the motile larvae, the (S1) larval stage. The state variable for this stage is the function $n_1(a, t)$, the density with respect to age per unit of volume. The two stages (J) (juvenile) and (M) (mature) are left unchanged, with the only restriction that they also are supposed to depend only on age and time.

We will now describe the passage through (S1). In doing this, we have to consider the food eaten by individuals in this stage from the beginning (entrance in (S1)). We assume that the passage to the next stage is subject to the condition for any individual to have eaten a certain amount of food Q_1 (threshold model). We denote $q_1(a, t)$ the amount of food eaten up to time t by an individual entered in (S1) a units of time earlier. We also assume that there is an upper limit T_1 to the time that an individual can spend in (S1). Individuals which have not acquired the amount Q_1 of food past time T_1 will die or never reach the next stage.

We denote $N_1(t) = \int_0^{T_1} n_1(a, t) da$, the population in stage (S1) which is susceptible to enter the next stage, at time t (per unit of volume). The variation of ingested food is governed by the following equation with zero boundary and initial conditions:

$$\begin{aligned} \frac{\partial}{\partial a} q_1(a, t) + \frac{\partial}{\partial t} q_1(a, t) &= \frac{K_1}{N_1(t) + C_1}, \\ q_1(0, t) &= 0, \\ q_1(a, 0) &= 0, \end{aligned} \tag{1}$$

K_1 is the quantity of food flowing into the species habitat per unit of volume, per unit of time. (For simplicity, K_1 is considered to be a constant and corresponds to the period when the phytoplankton is blooming.) C_1 represents the food (converted into a number of individuals) taken per unit of volume by consumers other than (S1) stage. Limitation of food due to density is modeled in the simplest possible way, assuming that the quantity of food available is shared in equal parts by all the individual occupying the same volume at time t . This is the interpretation of the term $K_1/(N_1(t) + C_1)$, which also incorporates a saturating effect in the case of low density. We assume implicitly that the S1 larvae who will not reach the next stage because they are still in S1 after age T_1 do not in fact compete for food. An implicit assumption underlying the

expression of the density dependence is that individuals of stage (S1) eating a specific food are not competing for this resource with other stages. The boundary condition $q_1(0, t) = 0$ is justified by the fact that age zero is the period when the individual has exhausted its yolk sac and has not eaten anything from the environment, yet. The initial condition $q_1(a, 0) = 0$ is justified by the fact that $t = 0$ is the first day of the reproduction period of a certain year. Note that $q_1(a, t)$ does not satisfy Eq. (1) for all $a, t > 0$. In fact, there is no individual in stage (S1) with age a in this stage larger than t , for it is a basic assumption of the model by Arino et al. [15], that larvae of a year do not survive as larvae the year after.

So, $q_1(a, t)$ has no meaning for $a > t$ or can just be assumed to equal zero in this region of the (a, t) -plane.

Integrating Eq. (1) along the characteristics lying in the region $t > a$ yields

$$q_1(a, t) = \int_{t-a}^t \frac{K_1}{N_1(\sigma) + C_1} d\sigma, \quad t > a. \tag{2}$$

Eq. (2) combined with the existence of the threshold Q_1 allows the computation of the time spent in (S1) in terms of the exit time. Throughout the paper, t is said to be an exit time (from a given stage) if there is a non-zero fraction of the population of that stage going at time t to the next stage. According to the assumption made here, a condition for t to be an exit time from the passive larval stage is that $q_1(T_1, t) > Q_1$.

Proposition 1. *For every exit time t , the time spent in (S1) is the number $a_1(t)$ defined by*

$$q_1(a_1(t), t) = Q_1. \tag{3}$$

The function a_1 is such that $t - a_1(t)$ is increasing on its domain. The domain of a_1 , the set of exit times, is, each year k , a union of intervals $[t_{\text{ext}}^0(k), t_{\text{ext}}^1(k)]$, where $t_{\text{ext}}^0(k)$ (respectively $t_{\text{ext}}^1(k)$) is the lowest (respectively, the highest) exit time out of (S1), at year k . For convenience, we will say that $a_1(t) = +\infty$, when t is not an exit time. So, instead of referring to the domain of a_1 , we may as well use the set of times t at which $a_1(t) < +\infty$.

Proof. Suppose t is an exit time. This implies that for some $a > 0, a < T_1$, we have $q_1(a, t) = Q_1$. The function $a \rightarrow q_1(a, t)$ is increasing. So, the above equation has at most one solution for a given t . So, if t is an exit time, there is one and only one number $a_1(t)$ such that Eq. (3) holds. One can differentiate $a_1(t)$ with respect to t . In view of formulae (2) and (3) one obtains

$$a_1'(t) = - \frac{\partial q_1(a_1(t), t) / \partial t}{\partial q_1(a_1(t), t) / \partial a} = - \frac{N_1(t - a_1(t)) - N_1(t)}{N_1(t) + C_1} \tag{4}$$

from which we obtain

$$1 - a_1'(t) = \frac{N_1(t - a_1(t)) + C_1}{N_1(t) + C_1} > 0. \quad (5)$$

So, the entry and the exit times are in monotonically increasing relationship. Given that the reproduction takes place each year k within a period $[k, k + t_1]$ the domain of a_1 , during each year k , lies in an interval $[t_{\text{ex}}^0(k), t_{\text{ex}}^1(k)]$ where $t_{\text{ex}}^0(k)$ is the solution of the equation: $t - a_1(t) = k$, and $t_{\text{ex}}^1(k)$ is the solution of $t - a_1(t) = k + t_1$. \square

We will now introduce another fundamental assumption of the model. We already said that in order for an individual to complete its stay in stage (S1), it is necessary that it has eaten a quantity Q_1 of food within a maximum time T_1 . We consider that the time that an individual can spend in (S1) is distributed according to a probability law. This hypothesis is an attempt to take into account individual resistance to fluctuation of food capacities. For example, one can imagine that a fraction f , $0 \leq f \leq 1$ of individuals have the ability of surviving a slow growth and completing stage (S1) by the time T_{large}^* after entering (S1) while the other $(1 - f)$ fraction die or will never leave (S1) if they have not eaten the quantity Q_1 by the time T_{small}^* , $T_{\text{small}}^* < T_{\text{large}}^*$. More generally, we assume there exists a function $f = f(a)$ such that, of N individuals of age a in (S1) which have not eaten the quantity Q_1 of food yet, the fraction $N \times f(a) da$ will die or lose the ability to go to the next stage within the age interval $]a, a + da[$.

In terms of the function $f(a)$ and the past residence time in (S1), $a_1(t)$, we can derive an equation for the density n_1 :

$$\begin{aligned} \frac{\partial}{\partial a} n_1(a, t) + \frac{\partial}{\partial t} n_1(a, t) &= -f(a)n_1(a, t), \quad 0 < a < a_1(t), \quad t > 0, \\ n_1(a, 0) &= 0, \\ n_1(0, t) &= B(t). \end{aligned} \quad (6)$$

From the definition of $a_1(t)$, we have

$$n_1(a, t) = 0 \quad \text{for } a > a_1(t). \quad (7)$$

In Eq. (6), the condition $n_1(a, 0) = 0$ expresses the fact that at $t = 0$, no individual is in stage (S1). The condition $n_1(0, t) = B(t)$ means that the recruitment in stage (S1) at time t is made of all the eggs produced at that time. Two simplified assumptions are needed for this: (1) No mortality of eggs is accounted for from birth to arrival in (S1). (2) Eggs produced at a given time enter the (S1) stage simultaneously. The right-hand side of the main equation in Eq. (6) is the mortality rate in (S1). We point out that the model accounts only for mortality due to the stochastic failure to complete (S1) stage in time. Other causes of mortality such as predation by adults are not considered. We will now determine the entrance in the motile larval stage. We have the following expression.

Proposition 2. *For the cohorts entering the (L) stage (for which $a_1(t) < +\infty$), we have*

$$L(0, t) = (1 - a'_1(t))n_1(a_1(t), t). \tag{8}$$

Proof. The formula is obtained by applying a book-keeping principle to those (S1) larvae which are susceptible to enter the next stage, that is to say, at a time t where $a_1(t) < +\infty$, their number $\bar{N}_1(t)$ is given by

$$\bar{N}_1(t) = \int_0^{a_1(t)} n_1(a, t) da.$$

By differentiating this formula, we obtain

$$\begin{aligned} \bar{N}'_1(t) &= n_1(a_1(t), t)a'_1(t) + \int_0^{a_1(t)} \frac{\partial}{\partial t} n_1(a, t) da, \\ \bar{N}'_1(t) &= n_1(a_1(t), t)a'_1(t) - [n_1(a, t)]_0^{a_1(t)} + \int_0^{a_1(t)} f(a)n_1(a, t) da, \\ \bar{N}'_1(t) &= -n_1(a_1(t), t)(1 - a'_1(t)) + n_1(0, t) - \int_0^{a_1(t)} f(a)n_1(a, t) da. \end{aligned}$$

The quantity $-n_1(a_1(t), t)(1 - a'_1(t))$ is the flow out and $B(t) = n_1(0, t)$ the flow in, yielding formula (8). \square

2.1. Dynamics of larvae

We stress the fact that the function $L(a, t)$ is connected to the motile larval stage, which we denote (L). We have the following:

$$\begin{aligned} \frac{\partial L(a, t)}{\partial a} + \frac{\partial L(a, t)}{\partial t} &= -\mu_L(a)L(a, t), \\ L(a, 0) &= 0, \\ L(0, t) &= (1 - a'_1(t))n_1(a_1(t), t); \quad L(0, t) = 0 \quad \text{if } a_1(t) = +\infty. \end{aligned} \tag{9}$$

The condition $L(a, 0) = 0$ corresponds to the assumption that no motile larva is present in the beginning of the year; $\mu_L(a)$ is the mortality rate in the larval stage.

Denoting $w(a, t)$ the size gained, since the moment they entered the (L) stage, until time t , by larvae whose age in that stage at time t is a , and g the size growth law as a function of the temperature and $\tilde{g}(t) = g(\mathcal{T}(t))$, where $\mathcal{T}(t)$ is the temperature at time t , we have

$$\frac{\partial w(a, t)}{\partial a} + \frac{\partial w(a, t)}{\partial t} = \tilde{g}(t) = g(\mathcal{T}(t)). \tag{10}$$

So,

$$w(a, t) = \int_{t-a}^t \tilde{g}(s) \, ds, \quad w(0, t) = 0. \quad (11)$$

We suppose that \tilde{g} is a positive continuous function. We exclude the possibility of time regression in size. Hence, size grows effectively during the larval stage period and we can evaluate the age of a larva reaching the threshold value $w = w^*$, either in terms of the birth date or in terms of the moment where the larva reaches this size. It is this last function which is given by the relation (11). We denote by $a^*(t)$ the unique function for which we have $w(a^*(t), t) = w^*$.

2.2. Dynamics of juveniles

The larvae that enter the juvenile phase at time t are those of age $a^*(t)$. Their density, with respect to time is given by the following formula.

Proposition 3. Denote by $J(a, t)$ the density of juveniles of age a at time t per unit of volume. Then,

$$J(0, t) = (1 - a^{*'}(t))L(a^*(t), t). \quad (12)$$

Proof. We can express the variation of the population in the (L) stage in two manners as in the case of the (S1) population in Proposition 1. We define $N_2(t) = \int_0^{a^*(t)} L(a, t) \, da$. $N_2(t)$ is the total number of motile larvae at time t . We compute $N_2'(t)$ in two ways. On the one hand, we have

$$N_2'(t) = -(1 - a^{*'}(t))L(a^*(t), t) + L(0, t) - \int_0^{a^*(t)} \mu_L(a)L(a, t) \, da, \quad (13)$$

this formula is obtained by differentiating the integral expression of $N_2(t)$ and using Eq. (9).

On the other hand we have

$$N_2'(t) = L(0, t) - J(0, t) - \int_0^{a^*(t)} \mu_L(a)L(a, t) \, da, \quad (14)$$

this formula is obtained by balancing the input and output rates and the mortality rate.

Comparing the expressions (13) and (14) of $N_2'(t)$ yields the desired formula for $J(0, t)$. \square

The dynamics of the juveniles is determined by the following equations:

$$\begin{aligned} \frac{\partial J(a, t)}{\partial a} + \frac{\partial J(a, t)}{\partial t} &= -\mu_J(a)J(a, t), \\ J(a, 0) &= J_0(a), \\ J(0, t) &= (1 - a^{*'}(t))L(a^*(t), t), \end{aligned} \quad (15)$$

where $J_0(a)$ is the distribution of juveniles at the year of reference (zeroth year) supposed to be known, $J(0, t)$ is the initial value given by Proposition 2 and $\mu_J(a)$ is the density of mortality rate of juveniles of age a .

2.3. Dynamics of adults

The adult stage starts when individuals become susceptible to participate in the reproduction. We make it start arbitrarily m years ($m = 2$ in the case of the population of sole) after the beginning of the juvenile stage. We will take into consideration only those of the juveniles becoming adults. We then obtain the following relation of transfer from juvenile stage to adult stage:

$$M(0, t) = J(m, t). \tag{16}$$

The dynamics of adults is described by the equations

$$\begin{aligned} \frac{\partial M(a, t)}{\partial a} + \frac{\partial M(a, t)}{\partial t} &= -\mu_M(a)M(a, t), \\ M(a, 0) &= M_0(a), \\ M(0, t) &= J(m, t), \end{aligned} \tag{17}$$

$M_0(a)$ is the distribution of adults at the year of reference (zeroth year) supposed known.

2.4. Production of eggs by adults

It is given by

$$B(t) = \int_0^{+\infty} \beta(a, t)e(a)M(a, t) da, \tag{18}$$

where $\beta(a, t)$ is the proportion of adults of age a at time t who are in position to give eggs. $e(a)$ is the number of eggs laid by adults of age a . Now, we are in position to derive the renewal equation and deduce the mathematical model describing the life cycle of the species.

3. The renewal equation

From now on, we will assume that $a_1(t) < +\infty$ for all t . This corresponds to the favorable environmental conditions that we mentioned in the Introduction. In this case, $\bar{N}_1 = N_1$.

Using the method of characteristics, we solve the equation governing the evolution of the population in the (S1) stage. It yields

$$n_1(a, t) = \begin{cases} \exp(-\int_0^a f(\sigma) d\sigma)B(t - a) & \text{for } a < t, \\ 0 & \text{for } a > t. \end{cases} \tag{19}$$

We integrate Eq. (8), using the method of characteristics

$$L(a, t) = \begin{cases} \exp\left(-\int_0^a \mu_L(\sigma) d\sigma\right)(1 - a'_1(t))n_1(a_1(t), t) & \text{for } a < t, \\ 0 & \text{for } a > t. \end{cases} \quad (20)$$

Replacing $n_1(a_1(t), t)$ by its expression given in Eq. (19), we obtain

$$L(a, t) = \begin{cases} \exp\left(-\int_0^a \mu_L(\sigma) d\sigma\right)(1 - a'_1(t))\exp\left(-\int_0^{a_1(t)} f(\sigma) d\sigma\right)B(t - a_1(t)) & \text{for } a < t, \\ 0 & \text{for } a > t. \end{cases} \quad (21)$$

Solving the equations of the juvenile stage in the same manner, we have

$$J(a, t) = \begin{cases} (1 - a^{*'}(t))L(a^*(t), t)\exp\left(-\int_0^a \mu_J(\sigma) d\sigma\right) & \text{for } a < t, \\ \exp\left(-\int_0^t \mu_J(\sigma) d\sigma\right)J_0(a - t) & \text{for } a > t. \end{cases} \quad (22)$$

Inserting the expression of $L(., .)$ given by Eq. (21) in the expression (22), we obtain

$$J(a, t) = \begin{cases} (1 - a^{*'}(t))\exp\left(-\int_0^a \mu_J(\sigma) d\sigma\right)\exp\left(-\int_0^{a^*(t)} \mu_L(\sigma) d\sigma\right) \\ (1 - a'_1(t))\exp\left(-\int_0^{a_1(t)} f(\sigma) d\sigma\right)B(t - a_1(t)) & \text{for } a < t, \\ \exp\left(-\int_0^t \mu_J(\sigma) d\sigma\right)J_0(a - t) & \text{for } a > t. \end{cases} \quad (23)$$

Solving the equations describing the adult stage by the method of characteristics, we have

$$M(a, t) = \begin{cases} \exp\left(-\int_0^a \mu_M(\sigma) d\sigma\right)M(0, t - a) & \text{for } t > a, \\ \exp\left(-\int_0^t \mu_M(\sigma) d\sigma\right)M_0(a - t) & \text{for } t < a. \end{cases} \quad (24)$$

So, by the relation of transfer from the juvenile to the larval stage, we have

$$M(a, t) = \begin{cases} \exp\left(-\int_0^a \mu_M(\sigma) d\sigma\right)(1 - a^{*'}(t - a))\exp\left(-\int_0^m \mu_J(\sigma) d\sigma\right) \\ \times \exp\left(-\int_0^{a^*(t-a)} \mu_L(\sigma) d\sigma\right)\exp\left(-\int_0^{a_1(t-a)} f(\sigma) d\sigma\right) \\ \times (1 - a'_1(t - a))B(t - a - a_1(t - a)) & \text{for } t - a > m, \\ \exp\left(-\int_0^t \mu_M(\sigma) d\sigma\right)\exp\left(-\int_0^{t-a} \mu_J(\sigma) d\sigma\right) \\ \times J_0(m - t + a) & \text{for } 0 < t - a < m, \\ \exp\left(-\int_0^t \mu_M(\sigma) d\sigma\right)M_0(a - t) & \text{for } t < a. \end{cases} \quad (25)$$

Thus, if we replace $M(a, t)$ by its expressions in Eq. (25) in the formula of $B(t)$ giving the egg production we deduce that

$$B(t) = \int_0^{t-m} \Phi(a, t, a_1(t-a))B(t-a-a_1(t-a)) da + \Theta(J_0, M_0)(t)$$

for $t > m$ (26)

where

$$\begin{aligned} \Phi(a, t, \alpha(\cdot)) = & \exp\left(-\int_0^a \mu_M(\sigma) d\sigma\right)(1 - a^{*t}(t-a)) \\ & \exp\left(-\int_0^m \mu_J(\sigma) d\sigma\right) \exp\left(-\int_0^{a^*(t-a)} \mu_L(\sigma) d\sigma\right)(1 - \alpha'(\cdot)) \\ & \exp\left(-\int_0^{\alpha(\cdot)} f(\sigma) d\sigma\right)\beta(a, t)e(a), \end{aligned}$$

(27)

$$\begin{aligned} \Theta(J_0, M_0)(t) = & \int_t^{+\infty} \beta(a, t)e(a) \exp\left(-\int_0^t \mu_M(\sigma) d\sigma\right)M_0(a-t) da \\ & + \int_{t-2}^t \beta(a, t)e(a) \exp\left(-\int_0^t \mu_M(\sigma) d\sigma\right) \\ & \exp\left(-\int_0^{t-a} \mu_J(\sigma) d\sigma\right)J_0(m-t+a) da \end{aligned}$$

(28)

and $a_1(t)$ satisfies

$$\int_{t-a_1(t)}^t \frac{K_1}{N_1(\sigma) + C_1} d\sigma = Q_1$$

(29)

with

$$N_1(t) = \int_0^{a_1(t)} \exp\left(-\int_0^a f(\sigma) d\sigma\right)B(t-a) da.$$

(30)

Hence, the model describing the life cycle of the population of fish considered here is given by the system of equations

$$\begin{aligned} B(t) = & \int_0^{t-m} \Phi(a, t, a_1(t-a))B(t-a-a_1(t-a)) da + \Theta(J_0, M_0)(t) \\ & \text{for } t > m, \\ N_1(t) = & \int_0^{a_1(t)} \exp\left(-\int_0^a f(\sigma) d\sigma\right)B(t-a) da, \\ Q_1 = & \int_{t-a_1(t)}^t \frac{K_1}{N_1(\sigma) + C_1} d\sigma, \end{aligned}$$

(31)

where Φ and Θ are given by formulas (26) and (27).

The model we have derived is complicated. The model can be simplified by disregarding the stages other than (S1) and establishing a direct connection from (S1) to the first generation to which (S1) contributes, r units of time later. This means that, from the production of eggs of a given year, we are just taking into account those laid by the adults laying for the first time this given year. The possibility to discriminate this production is substantiated by field observations, made on fish species that migrate to spawning areas, such as the sole, showing that the older ones tend to arrive earlier in the spawning areas and lay eggs earlier. So, by restricting $B(t)$ to part of the reproduction season, one can assume, with of course some uncertainty, that this fraction of the new born has been laid by the adults of the first adult age class (31).

4. A simplified model

We assume that we can determine the eggs of a given year directly in terms of the passive larvae that survived some years earlier. This is a crude assumption which, however, may find some justification in some cases: for example, for the anchovy of the Bay of Biscay, it is known that most of the reproduction which takes place near some of the estuaries is due to the one-year class. So, in this case, there is a strong relationship between the eggs of a given year and those of one year later [31]. The simplified model reads

$$\begin{array}{ccc}
 (B) & \xrightarrow{r} & ((S1)) \\
 \uparrow & r \text{ units of time} & \downarrow \\
 & \overleftarrow{t+r} &
 \end{array} \tag{32}$$

We assume the simplest type of relation:

$$B(t+r) = k(t)N_1(t). \tag{33}$$

Replacing $B(t)$ by its expression in Eq. (33) in the equation of $N_1(t)$ in Eq. (31), we obtain

$$N_1(t) = \int_0^{a_1(t)} \exp\left(-\int_0^a f(\sigma) d\sigma\right) k(t-r-a)N_1(t-r-a) da, \tag{34}$$

coupled with the equation

$$\int_{t-a_1(t)}^t \frac{K_1}{N_1(\sigma) + C_1} d\sigma = Q_1.$$

If we suppose that $k(t) = k = \text{constant}$, we have the simplified model

$$\begin{aligned}
 N_1(t) &= \int_0^{a_1(t)} \exp\left(-\int_0^a f(\sigma) d\sigma\right) kN_1(t-r-a) da, \\
 \int_{t-a_1(t)}^t \frac{K_1}{N_1(\sigma) + C_1} d\sigma &= Q_1,
 \end{aligned} \tag{35}$$

which can be written in the form

$$\begin{aligned}
 N_1(t) &= k \int_{t-a_1(t)}^t \exp\left(-\int_0^{t-a} f(\sigma) d\sigma\right) N_1(a-r) da, \\
 \int_{t-a_1(t)}^t \frac{K_1}{N_1(\sigma) + C_1} d\sigma &= Q_1.
 \end{aligned}
 \tag{36}$$

One can differentiate equations in system (36) and obtain

$$\begin{aligned}
 N_1'(t) &= kN_1(t-r) - (1-a_1'(t)) \exp\left(-\int_0^{a_1(t)} f(\sigma) d\sigma\right) kN_1(t-r) \\
 &\quad - k \int_{t-a_1(t)}^t f(t-a) \exp\left(-\int_0^{t-a} f(\sigma) d\sigma\right) N_1(a-r) da, \\
 a_1'(t) &= \frac{N_1(t) - N_1(t-a_1(t))}{N_1(t) + C_1}.
 \end{aligned}
 \tag{37}$$

4.1. A few considerations regarding the model

Eq. (37) is a system of delay differential equations in which one of the delays, $a_1(t)$, is itself a solution of an ordinary differential equation whose coefficients are functions of the state. In short, one calls such an equation a state-dependent delay differential equation, although this denomination covers a wide variety of situations. Such equations can be found in the literature, associated with a wealth of applications. See, for example, Ref. [32] for a short survey of applications. Usually, the state-dependent delay is motivated by phenomenological considerations: in Ref. [33], such a delay is justified as a response of the maturation processes to density-dependence. We want to emphasize the fact that it is not the way that this occurs in our model. The main cause for state-dependent delay is the threshold condition (3). The investigation of mathematical properties of such systems is relatively recent. For equations of the type (37), the only results we are aware of are those in Ref. [20]. With some simplifications, we may consider system (37) as a model valid over several years. Thus, the study of long term behavior of system (37) may give information about the behavior of a fishery over years. This requires the study of mathematical properties of system (37), which is currently undertaken and will be presented elsewhere. Here, we will restrict ourselves to a few simple considerations.

First of all, looking at the equation verified by $a_1(t)$, we note that the variations of the sign of $a_1'(t)$ are related to rather long-lasting changes of the density of (S1) stage, that is, it is not sufficient that the density goes down for the competition pressure to go down immediately; it is necessary that the downwards movement lasts for a period of the order of the duration of the (S1) stage.

Let us next examine some special situations where the analysis of (S1) is facilitated and however allows to draw interesting conclusions. Using the inequality

$$\frac{K_1}{N_1(t) + C_1} \leq \frac{K_1}{C_1} \quad (38)$$

in relations (2) and (3), one arrives at

$$a_1(t) \geq \frac{Q_1 C_1}{K_1},$$

which gives a lower bound to the duration of the early larval stage. In terms of T_1 , we obtain the following:

$$T_1 \geq \frac{Q_1 C_1}{K_1}. \quad (39)$$

Inequality (39) provides an easy-to-interpret condition for the survival of larvae through the (S1) stage.

We now examine the situation where $N_1(t) \ll C_1$. In this case,

$$q_1(a, t) \simeq \frac{K_1}{C_1} a, \quad (40)$$

that is to say,

$$a_1(t) \simeq \frac{Q_1 C_1}{K_1} \simeq \bar{a}_1. \quad (41)$$

So, in this case, the duration of (S1) is constant. Assuming for simplicity that $f(a) = \bar{f}$ one can deduce from Eq. (6) an estimate of the probability of recruitment into the active larval stage, from the egg stage:

$$\frac{L(0, t)}{B(t - a_1)} \simeq \exp\left(-\frac{\bar{f} Q_1 C_1}{K_1}\right). \quad (42)$$

Formula (42) shows the following: in the case $N_1(t) \ll C_1$, that is, when the (S1) larvae are in relatively low abundance in the plankton, and at the same time the food share is large enough, then the death process during the (S1) stage is essentially the natural mortality. The situation changes if we assume that the (S1) larvae are relatively abundant or/and the food share is low. Further consequences could be drawn from further investigation of the model.

5. Discussion

We have described a model for the growth and survival of a population of fish in the early larval stage. The model fits, in principle, species for which the larval stage is pelagic. It is in the line of a previous model for the sole of the bay of Biscay, described in Ref. [15], but we may also think of the anchovy. The life

history of the fish is divided into five stages: eggs, passive larvae (S1), active larvae (L), the juveniles (J) and the adults (M). Each stage but the first one is structured by the age (in the stage). The exit from the two larval stages is subject to the accumulation of a threshold amount of food eaten in each of the stages. We have introduced a density-dependence effect during (S1), assuming essentially that animals occupying a given volume tend to share the food inside the volume equally. This last assumption is certainly not correct. One should probably take into account the age of the individuals. Modifying the model accordingly is not a problem. For an easier presentation, we limited ourselves to the equal share model. We derived a renewal equation and, using a short-cut path from the end of the (S1) stage to the next generation of eggs (as shown in (32)), we presented a simplified version of that equation, that is, a system of two state delay differential equations. As far as we know there is no example of such a system in the literature. The study of the system is out of the scope of the paper. A similar system was considered recently by Arino et al. [20]. In the introduction, we have supplied a brief comparison with other approaches. However, a quantitative comparison, based on how our model fits data, is premature.

For the time being, the main issue is theoretical: what is the level of detail necessary and sufficient for a model to have a chance of being useful? We believe that models should incorporate as much biology, demography, and oceanography, as they can bear. This was the idea followed in Ref. [15]. The present work is a continuation of the latter paper, concentrating on the passive larval stage.

Let us now discuss the conditions under which the description of the (S1) stage is valid. In the introduction, we mention a scenario: mild steady weather conditions which favor the production of well mixed patches of plankton inside which the main mechanism controlling early larvae growth is the presence of other larvae and possibly other species with which they have to share the food. As long as such conditions prevail, one can neglect spatial effects; one also neglects predation. In fact, we consider that predation has already taken effect and the relative density of (S1) larvae in the plankton is rather low. What, if the weather conditions were worsening? It is then a common belief that bad weather conditions over a certain period of time tend to disrupt plankton patches. Early larvae having not yet completed the (S1) stage may then find themselves in a poor environment and have a high risk of starving to death. We have not included this catastrophic event in our scenario. We are presently working on how to model such events.

Let us briefly comment on the model in its whole. A distinguishing feature of the model is that besides the egg stage, we divide the life cycle of the fish into a passive phase, which coincides with (S1) and an active phase, which comprises an advanced larval stage and the juvenile and the mature stages. Whenever (S1) should be started on is probably a matter of controversy. In his monograph [1],

Horwood mentions that prelarvae, still in the yolk-sac stage, are starting to feed on prey. No doubt however that there is a possibly short period during which the larvae can be viewed as passive filtering systems, whose survival is tightly dependent upon the abundance of food in their immediate surrounding. As soon as the larva becomes active, it is able to swim in a larger area in the quest of food. Density-dependence effects are then secondary, although patches of advanced larvae and even juveniles or adults have been observed. So, the feeding area of active larvae is significantly bigger than the one of (S1) larvae, thus their food uptake depends on the plankton availability in a larger area. So, the instant growth rate of active larvae is somehow legitimately related to the average plankton resource in a large area: this is the idea behind Eq. (10). Finally, the juvenile and the mature stages were described as only age dependent processes. This, of course, is a simplification: frequent observations have been made about the relationship between the size of adults and the spawning period or even the spawning location [31]. This fact however does not play an essential role in the description of the larval stage, which was the main purpose of this work. Further consideration will be given to it in future work.

5.1. Conclusion

As a general conclusion, we comment now on the interest of such a work. Modelling fish dynamics is indeed a very difficult task. It is a highly interdisciplinary subject with demographic, biological and oceanographical aspects. As yet, there is no satisfactory model. One could consider that, since it is so difficult, it would be practical to forget about models. But, models are necessary when evaluating the resources. Measurements made in the field for evaluation purposes are just samples. Models play a fundamental role when passing from samples to life-size scale. So, it is in fact necessary to continue developing models. This should be done using all possible ways of building models. Notably, mathematical models may play a role. However, it is crucial that model building be undertaken with the collaboration of biologists, experts on fish, fisheries and oceanography. The present work was elaborated along this line of thought. It is a first step which will be followed by further developments.

Acknowledgements

O.A. was partially supported by a grant from IFREMER, contract 955511002, contract 965510028; O.A. and R.B. were partially supported by a joint programme France–Spain (AI 96/001); M.L.H. was partially supported by a joint programme France–Morocco (AI 95/0850). The authors benefitted from discussions with Y. Desaunay (IFREMER), C. Koutsikopoulos (University of Patras, Greece), F. Lagardère (CREMA, CNRS) and P. Prouzet (IF-

REMER). The authors express their sincere thanks to two anonymous referees for their remarks and for attracting their attention to interesting references, and to the Editor of Mathematical Biosciences for his encouragements.

References

- [1] J. Horwood, The Bristol channel sole (*Solea solea* (L.)): A fisheries case study, *Adv. Marine Biol.* 29 (1993) 215.
- [2] W.C. Leggett, E. Deblois, Recruitment in marine fishes: Is it regulated by starvation and predation in the eggs and larval stages?, *Netherlands J. Sea Res.* 32 (1994) 119.
- [3] J. Hjort, Fluctuations in the great fisheries of northern Europe reviewed in the light of biological research, *ICES Rap. Proc.-Verb* 20 (1914) 1.
- [4] D.H. Cushing, *Marine Ecology and Fisheries*, Cambridge University, Cambridge, 1975.
- [5] B.R. MacKenzie, W.C. Leggett, R.H. Peters, Estimating larval fish ingestion rates: Can laboratory derived values be reliably extrapolated to the wild?, *Mar. Eco. Prog. Ser.* 67 (1990) 209.
- [6] S. Regner, Ecology of planktonic stages of the anchovy, *Acta Adriat.* 26 (1985) 5.
- [7] L. Fortier, A. Villeneuve, Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*: Trophodynamics and potential impact on recruitment, *Fish. Bull.* 94 (1996) 268.
- [8] P. Fossum, A tentative method to estimate mortality in the egg and early fish larval stages, with special reference to cod (*Gadus morhua* L.), *Fisker. Skr. Ser. Havunders* 18 (1988) 329.
- [9] L. Incze, D. Campbell, Estimation of ichthyoplankton (*Theragra chalcogramma*) mortality rates from a patch study: FOCI 1986, Bigelow Laboratory for Sciences, Tech. Rep. 72, 1989, 10+XXX1p.
- [10] S.E. Dorsey, E.D. Houde, J.C. Gamble, Cohort abundances and daily variability in mortality of eggs and yolk-sac larvae of bay anchovy *Anchoa mitchilli*, in Chesapeake Bay, *Fish. Bull.* 94 (1996) 257.
- [11] J. Hjort, Fluctuations in the year classes of important food fishes, *J. Cons.* 1 (1926) 5.
- [12] C.P. O'Connell, Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods, *Fish. Bull.* 78 (1980) 475.
- [13] K.M. Bailey, E.D. Houde, Predation on eggs and larvae of marine fishes and the recruitment problem, *Adv. Marine Biol.* 25 (1989) 1.
- [14] F. Lagardère, Expérience de fermeture d'une baie à l'exploitation, personal communication, 1996.
- [15] O. Arino, C. Koutsikopoulos, A. Ramzi, Elements of mathematical modeling of the evolution in number of a sole population, *J. Biol. Systems* 4 (1996) 445.
- [16] M. Schaefer, Some aspects of the dynamics population important to the management of the commercial marine fisheries, *Bull. Int. Amer. Trop. Tuna. Comm.* 1/2 (1954) 26.
- [17] W.E. Ricker, Computation and interpretation of biological statistics of fish populations, *Bull. Fish. Res. Bord. Can.* 191 (1958) 1.
- [18] J.J. Pella, P.K. Tomlinson, A generalized stock production model, *Bull. IATTC* 13 (1969) 419.
- [19] R.J.H. Beverton, S.J. Holt, On the dynamics of exploited fish population, in: U.K. Min. Agric., *Fish. Food, Fisheries Investigations Series*, vol. 2, 1957, p. 19.
- [20] O. Arino, K.P. Hadeler, M.L. Hbid, Existence of periodic solutions of delay differential equations with state dependent delay, submitted.
- [21] J.A.J. Metz, O. Diekmann, The dynamics of physiologically structured populations, in: *Lecture Notes in Biomathematics*, vol. 68, Springer, Berlin, 1986.

- [22] W.E. Ricker, R.E. Foerster, Computation of fish production, *Bull. Bingham Oceanogr. Coll.* 11 (1948) 173.
- [23] J. Shepherd, D.H. Cushing, A mechanism for density dependent survival of larval fish as the basis of stock-recruitment relationship, *J. Cons. Int. Explor. Mer.* 39 (1980) 160.
- [24] J.E. Beyer, Recruitment stability and survival – Simple size-specific theory with examples from the early life dynamics of marine fish, *Dana* 7 (1989) 45.
- [25] E.D. Houde, Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects, *Fish. Bull.* 87 (1989) 471.
- [26] M. Huston, D. DeAngelis, W. Post, New computer models unify ecological theory, *BioScience* 38 (1988) 682.
- [27] D.L. DeAngelis, L. Godabout, B.J. Shuter, An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations, *Ecol. Modelling* 57 (1991) 91.
- [28] D.L. DeAngelis, B.J. Shuter, M.S. Ridgely, M. Schaefer, Modelling growth and survival in an age-0 fish cohort, *Trans. Amer. Fish. Soc.* 122 (1993) 927.
- [29] G. Champalbert, C. Koutsikopoulos, Behavior, transport and recruitment of the Bay of Biscay sole (*Solea solea* (L.)): Laboratory and field studies, *J. Mar. Biol. Ass. U.K.* 75 (1995) 93.
- [30] C. Koutsikopoulos, Y. Desaunay, D. Dorel, J. Marchand, The role of coastal areas in the life history of sole (*Solea solea* L.) in the Bay of Biscay, in: J.D. Ros (Ed.), *Topics in Marine Biology*, *Scient. Mar.* 53 (1989) 567.
- [31] L. Motos, A. Uriarte, V. Valencia, The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus* L.), Preprint, 1996.
- [32] J. Bélair, Population models with state-dependent delay, in: O. Arino, D. Axelrod, M. Kimmel (Eds.), *Proceedings of the Second International Conference Mathematical Population Dynamics*, *Lecture Notes in Pure and Applied Mathematics*, vol. 131, Marcel Dekker, New York, 1991, p. 165.
- [33] W.G. Aiello, H.I. Freedman, J. Wu, Analysis of a model representing stage-structured population growth with state-dependent time delay, *SIAM J. Appl. Math.* 52 (1992) 855.